

NOTE / NOTE

Minimal overwintering temperatures of red-sided garter snakes (*Thamnophis sirtalis parietalis*): a possible cue for emergence?

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Abstract: Red-sided garter snakes (*Thamnophis sirtalis parietalis* (Say in James, 1823)) in Manitoba, Canada, undergo 8 months of continuous winter dormancy prior to spring emergence. As in other ectothermic species, increases in ground temperature may be the cue for emergence from winter dormancy in these populations. To test this hypothesis, we measured body temperatures during winter dormancy by surgically implanting small temperature loggers into 32 female red-sided garter snakes before they entered their native hibernaculum. The following spring, we recaptured seven of the snakes implanted with temperature loggers. Body temperature declined gradually from mid-September (14.7 ± 0.24 °C, mean \pm SE) to early April (1.1 ± 0.16 °C, mean \pm SE) during winter dormancy, reaching minimal values approximately 1 month prior to spring emergence. Body temperatures of emerging snakes ranged from 0.5 °C during early spring to 6.3 °C during late spring (3.4 ± 0.84 °C, mean \pm SE). These results do not support the hypothesis that an increase in ground temperature (and hence body temperature) is necessary for emergence from winter dormancy. We suggest that critically low temperatures (i.e., 0.5–1 °C) are a Zeitgeber entraining an endogenous circannual cycle that regulates snake emergence. These results offer new insight into the mechanisms regulating seasonal emergence from winter dormancy.

Résumé : Les couleuvres rayées à flancs rouges (*Thamnophis sirtalis parietalis* (Say in James, 1823)) du Manitoba, Canada, complètent 8 mois continus de dormance d'hiver avant leur émergence au printemps. Comme c'est le cas chez d'autres espèces ectothermes, l'accroissement de la température du sol est peut-être le signal pour l'émergence de la dormance hivernale chez ces populations. Afin de vérifier cette hypothèse, nous avons mesuré la température corporelle de 32 couleuvres rayées à flancs rouges femelles durant la dormance d'hiver en leur insérant par chirurgie de petits enregistreurs de température avant qu'elles n'entrent dans leurs hibernacles d'origine. Le printemps suivant, nous avons récupéré sept des couleuvres porteuses d'enregistreurs de température. La température corporelle décline graduellement de la mi-septembre ($14,7 \pm 0,24$ °C, moyenne \pm erreur type) au début d'avril ($1,1 \pm 0,16$ °C, moyenne \pm erreur type) durant la dormance d'hiver, atteignant un minimum environ un mois avant l'émergence printanière. La température corporelle des couleuvres à l'émergence varie de 0,5 °C au début du printemps à 6,3 °C à la fin du printemps ($3,4 \pm 0,84$ °C, moyenne \pm erreur type). Ces résultats n'appuient pas l'hypothèse qui veut qu'un accroissement de la température du sol (et par conséquent de la température corporelle) soit nécessaire pour l'émergence de la dormance d'hiver. Nous croyons que les températures basses critiques (c.-à-d., 0,5–1 °C) agissent comme Zeitgeber pour établir un cycle circannuel qui règle l'émergence des couleuvres. Ces résultats ouvrent de nouvelles perspectives sur les mécanismes régulateurs de l'émergence saisonnière de la dormance d'hiver.

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Introduction

Most vertebrates exhibit some seasonality in many behavioral and physiological processes. One of the most reliable environmental cues thought to function in regulating seasonality in vertebrates is photoperiod. Unlike other environmental signals (e.g., temperature and humidity) that can vary quite dramatically both within seasons and among years,

changes in photoperiod length accurately and reliably reflect changing environmental seasons. Many ectotherms inhabiting north-temperate climates, however, undergo periods of prolonged winter dormancy prior to spring breeding. Animals that occupy underground hibernacula during winter dormancy are not exposed, or receive little exposure, to changing photoperiodic conditions (e.g., Whittier et al. 1987; Grobman 1990). Thus, photoperiod is likely not a critical

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factor in synchronizing spring emergence from overwintering locations. For example, photoperiod prior to and during winter dormancy has no influence on the initiation and timing of reproductive behavior of red-sided garter snakes (*Thamnophis sirtalis parietalis* (Say in James, 1823)) upon spring emergence (Nelson et al. 1987; Whittier et al. 1987). Rather, temperature appears to be the most important environmental cue for synchronizing reproduction in reptiles (Licht 1972, 1984; Duvall et al. 1982; Whittier et al. 1987).

In some ectothermic species, increases in ambient and ground temperatures during spring are thought to play a role in initiating emergence from winter dormancy and subsequent reproductive behavior (e.g., Hawley and Aleksiuk 1975, 1976; Jacob and Painter 1980; Crews and Garstka 1982; Licht 1984; Whittier et al. 1987; Macartney et al. 1989; Crawford 1991). For example, emergence from winter dormancy in the box turtles *Terrapene carolina* (L., 1758) and *Terrapene ornata* (Agassiz, 1857) occurs after subsurface ground temperatures increase for several consecutive days (Grobman 1990). Emergence of northern Pacific rattlesnakes (*Crotalus oreganus oreganus* (Holbrook, 1840)) also occurs as hibernaculum temperatures increase (Macartney et al. 1989). Etheridge et al. (1983) demonstrated experimentally that increasing ambient temperatures stimulate emergence of the six-lined racerunner (*Cnemidophorus sexlineatus* (L., 1766)) from winter dormancy. However, some ectothermic species (especially those inhabiting extreme northern latitudes) can occupy underground dens at depths where ground temperatures do not change significantly prior to spring emergence (e.g., Macartney et al. 1989), suggesting that increases in ground temperatures may not be the only thermal cue used by reptiles.

To better understand the environmental cues regulating spring emergence and reproduction in reptiles, we measured body temperatures of red-sided garter snakes during winter dormancy under natural field conditions. Red-sided garter snakes are the most northerly living reptile in North America and are found in extremely large numbers throughout south-central Manitoba, Canada. These northern-latitude populations of snakes undergo a period of continuous winter dormancy for approximately 8 months each year. Following spring emergence, an attenuated mating season lasting approximately 4–5 weeks is initiated (e.g., Crews and Garstka 1982). In this well-studied dissociated breeder, mating behavior is triggered by increases in environmental temperatures following winter dormancy (Ross and Crews 1978; Garstka et al. 1982; Bona-Gallo and Licht 1983; Krohmer and Crews 1987; Whittier et al. 1987).

Given the unique life history traits of these snake populations, temperature is likely the most important proximate environmental cue governing the initiation of emergence from winter dormancy. Previous studies investigating the role of temperature in regulating spring emergence in red-sided garter snakes were conducted in the laboratory (e.g., Bona-Gallo and Licht 1983; Krohmer and Crews 1987; Whittier et al. 1987). Furthermore, these studies focused on the role of temperature in initiating reproductive behavior, as it is a more conspicuous end point to measure. There are limited data regarding overwintering temperatures of ectotherms under natural field conditions, especially in northern lati-

tudes. In addition, few field studies have focused on the thermal cues regulating spring emergence. We examined the efficacy of temperature as an important cue for synchronizing spring emergence under natural field conditions. Specifically, we sought to determine if hibernaculum temperatures (and hence snake body temperatures) increase significantly prior to emergence from winter dormancy. Because the initiation of spring emergence of red-sided garter snakes is independent of changes in photoperiodic conditions (Nelson et al. 1987; Whittier et al. 1987), this model system provides an excellent opportunity to examine the role of temperature as the primary environmental cue synchronizing emergence from prolonged winter dormancy.

Materials and methods

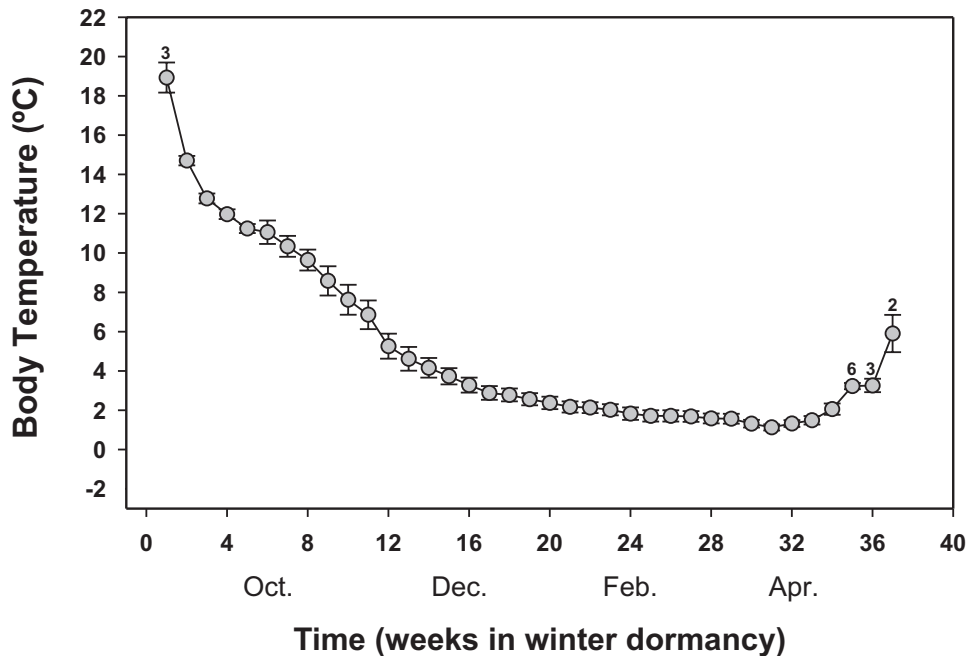
Experiments were conducted in the field with free-ranging red-sided garter snakes in the Interlake region of Manitoba, Canada (50°30'N, 97°30'W). All experimental protocols were approved by the Oregon State University Animal Care and Use Committee (protocol No. 2661) and were in accordance with the *Guide for the Care and Use of Laboratory Animals* (National Institutes of Health 1985). This research was approved by the Manitoba Wildlife Animal Care Committee (protocol No. 2002-06) and was performed under the authority of Manitoba Wildlife scientific permit No. WSP 03009.

Similar to Grayson and Dorcas (2004) and Angilletta and Krochmal (2003), we measured body temperatures of red-sided garter snakes during winter dormancy by surgically implanting snakes with small temperature loggers (Thermochron iButton; Dallas Semiconductor, Dallas, Texas). Data loggers were programmed to sample temperature once every 3 h using the 32-Bit iButton-TMEX Runtime Environment software (Dallas Semiconductor, Dallas, Texas). This sampling rate was used to ensure continuous recordings of body temperatures throughout the 8-month dormancy period (i.e., for approximately 256 days). The sampling times of all data loggers were synchronized so that body temperatures of individual snakes were recorded at the same time of day.

Thirty-two female red-sided garter snakes having a snout-vent length ≥ 62 cm (71.2 ± 0.78 cm, mean \pm SE) were collected in the fall (9–15 September 2003) after snakes returned to the den site to overwinter. Female snakes were used in this study because of their much larger body size. Snakes were anesthetized with sodium brevaltal (0.003 mL of 0.5% (m/v) brevaltal/g body mass) and a temperature logger was surgically implanted into the peritoneal cavity. Data loggers (17.4 mm diameter \times 5.7 mm height, 3.1 g) were 2.2% of the mean body mass of snakes (range = 2.8% of the smallest snake to 1.4% of the largest snake) and produced a slight, noticeable bulge in the midbody area containing the temperature logger. To aid in recapture of female snakes during the spring when they are emerging among thousands of garter snakes, we individually scale-clipped each snake with a unique number and a silver sequin was secured to the parietal scales with glue. Snakes were allowed to recover from surgery for 1–5 days before being released at the site of capture, where they were allowed to hibernate under natural conditions.

The following spring, we recaptured seven of the snakes implanted with temperature loggers. We attribute this recap-

Fig. 1. Body temperatures of female red-sided garter snakes (*Thamnophis sirtalis parietalis*) during winter dormancy in dens under natural field conditions in Manitoba, Canada. Unless otherwise noted by sample sizes above the SE bars, each data point is a weekly mean \pm 1 SE of 7 snakes.



ture rate to the difficulty of locating snakes among the extremely large numbers of snakes (~35 000; Shine et al. 2006) at this den site. Mortality may have contributed to reducing the number of females recaptured, but mortality rates of red-sided garter snakes during winter dormancy in the field are unknown. All females were captured immediately following emergence from the hibernaculum and the specific time and date of capture were recorded for each snake. The temperature loggers were surgically removed and the females were released at the site of capture following recovery; data were downloaded for analysis. Only body temperature data for snakes prior to complete emergence were used in the analyses of winter dormancy temperatures.

Ground temperatures were measured during the period of winter dormancy at six different soil depths (0, 0.3, 0.6, 0.9, 1.2, and 1.5 m) using Thermochron iButton temperature loggers. Data loggers were programmed to sample temperature once every 3 h and synchronized with the data loggers recording body temperatures of female snakes. To protect the data loggers from groundwater during the observation period, we sealed each iButton in a small balloon (not inflated) before placement in the ground. Owing to the rocky terrain at the den site and because the den site is located on public property, ground temperatures were measured at the field station approximately 20 km north of the den (50°37'N, 97°32'W). To aid in the retrieval of temperature loggers in the spring, we first dug a hole 1.5 m deep by inserting a metal cylinder into the ground. Temperature loggers were then placed into the ground at 0.3 m intervals. To mimic the rocky terrain at the den site, we used gravel to fill the spaces between data loggers and placed rocks over the site. Mean high and low ambient temperatures during September 2003 through May 2004 were obtained for a nearby area (Lundar, Manitoba; 50°43'N, 97°51'W) from Environment Canada.

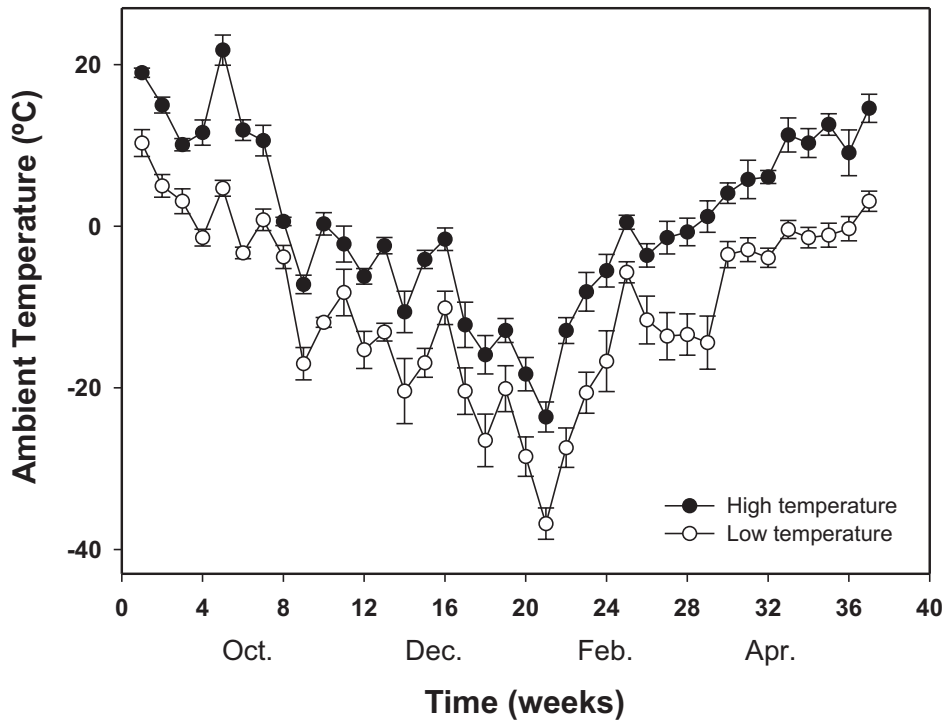
All data are reported as means \pm SE, unless otherwise indicated.

Results

Body temperatures of female red-sided garter snakes declined gradually from mid-September (14.7 ± 0.24 °C) to early April (1.1 ± 0.16 °C) during the 8-month dormancy period (Fig. 1). Body temperatures did not reach minimal values until April, approximately 1 month prior to the beginning of spring emergence. Mean body temperature of snakes 1 week prior to emergence was 2.6 ± 0.39 °C. Mean body temperature of snakes 1 day prior to emergence was 3.4 ± 0.84 °C. Because female garter snakes emerge over the entire 4-week mating season, mean body temperature 1 day prior to emergence ranged from 0.5 °C when snakes emerged during early spring to 6.3 °C when snakes emerged during late spring. Prehibernation body mass of snakes was significantly higher than posthibernation body mass ($P < 0.001$ from a paired t test; data not shown). The mean percent body mass loss of female snakes during winter dormancy was $10.4\% \pm 1.6\%$.

Mean high ambient temperatures were below 0 °C from late October through late March (Fig. 2). Although the underground hibernaculum protected snakes from ambient temperatures, snakes could only escape freezing temperatures at a depth of 1.2 m or greater (Fig. 3). Groundwater was observed at soil depths of 1.2 and 1.5 m during retrieval of the ground temperature dataloggers. During the period of spring emergence (i.e., from 29 April to 22 May, weeks 34–37 of winter dormancy), ground temperatures at depths of 1.2 and 1.5 m increased by only 3.0 and 2.5 °C, respectively (Fig. 3).

Fig. 2. Mean high and low ambient temperatures from September 2003 to May 2004 (i.e., during the dormancy period of red-sided garter snakes). Data were obtained for a nearby area from Environment Canada. Each data point is a weekly mean \pm 1 SE.



Discussion

Our results indicate that red-sided garter snakes near the northern limit of this species' range in Manitoba, Canada, have a mean minimum body temperature of 1.1 ± 0.16 °C during winter dormancy. This body temperature is much lower than that estimated previously for these populations of snakes during hibernation (i.e., 3–6 °C; Whittier et al. 1987). The range of body temperatures that we observed during winter dormancy is similar to that reported by Macartney et al. (1989), who measured body temperatures of red-sided garter snakes in a communal den in northern Alberta, Canada. However, owing to the failure of the radiotelemetry equipment, body temperatures of only one red-sided garter snake could be monitored (Macartney et al. 1989). The mean body temperature of this snake during hibernation was 3.9 ± 0.34 °C (mean \pm SE; $n = 16$ observations during hibernation); body temperature ranged from 1.8 to 6.5 °C (Macartney et al. 1989).

Body temperatures of snakes remained above 0 °C throughout winter dormancy and were similar to ground temperatures observed at a depth of 1.5 m from November through late April (weeks 12–33; Fig. 4). These results support previous findings that garter snakes cannot endure prolonged freezing stress (reviewed in Storey and Storey 1992) and instead seek thermally buffered hibernaculum sites. It is evident that ambient temperatures directly influence hibernaculum temperatures during the dormancy period, especially at shallower hibernaculum depths (Figs. 2, 3). Ground temperature measurements indicate that snakes must have moved to a depth of at least 1.2 m below the den surface to escape freezing temperatures (Fig. 3). At depths of 1.2 and 1.5 m, ground temperatures decreased gradually

but were fairly stable during the period of winter dormancy; ground temperatures at these soil depths increased no more than 3 °C during the period of spring emergence (weeks 34–37; Fig. 3).

An increase in hibernaculum temperatures could potentially be a cue for emergence, but the underlying mechanism must be sensitive to very small changes in temperature (i.e., 2.5–3.0 °C) over a period of <1 month. Similar patterns of spring emergence have been observed in the box turtles *T. carolina* and *T. ornata* (Grobman 1990). Spring emergence (and subsequent reproductive behavior) of red-sided garter snakes may be controlled by an endogenous circannual rhythm that is entrained by the slight increase in ground temperatures observed during this study (e.g., Licht 1972; Gregory 1982).

In contrast, some snakes were observed to emerge from the hibernaculum without a significant increase in body temperature. These results therefore do not support the hypothesis that an increase in ground temperature (and therefore body temperature) is a necessary cue for emergence from winter dormancy. For example, during early to mid-May, two snakes emerged at a body temperature of only 0.5 °C. These observations are similar to those reported by Macartney et al. (1989), who also observed cloacal temperatures as low as 0.5 °C in emerging garter snakes. In late May, however, body temperatures of emerging snakes were as high as 6.3 °C. This higher body temperature at emergence is likely attributable to the higher ground temperatures experienced at the hibernaculum surface as snakes emerged later in the season (Fig. 3). During the period of spring emergence (May, weeks 34–37), ground temperatures at depths of 1.2 and 1.5 m did not increase above 4 °C. Thus, snakes (i.e., ectotherms) with body temperatures higher than 4 °C prior to

Fig. 3. Ground temperatures during the dormancy period of red-sided garter snakes at six different soil depths (0, 0.3, 0.6, 0.9, 1.2, and 1.5 m). Temperatures were measured at a site near the snake hibernaculum. Each data point is a weekly mean \pm 1 SE.

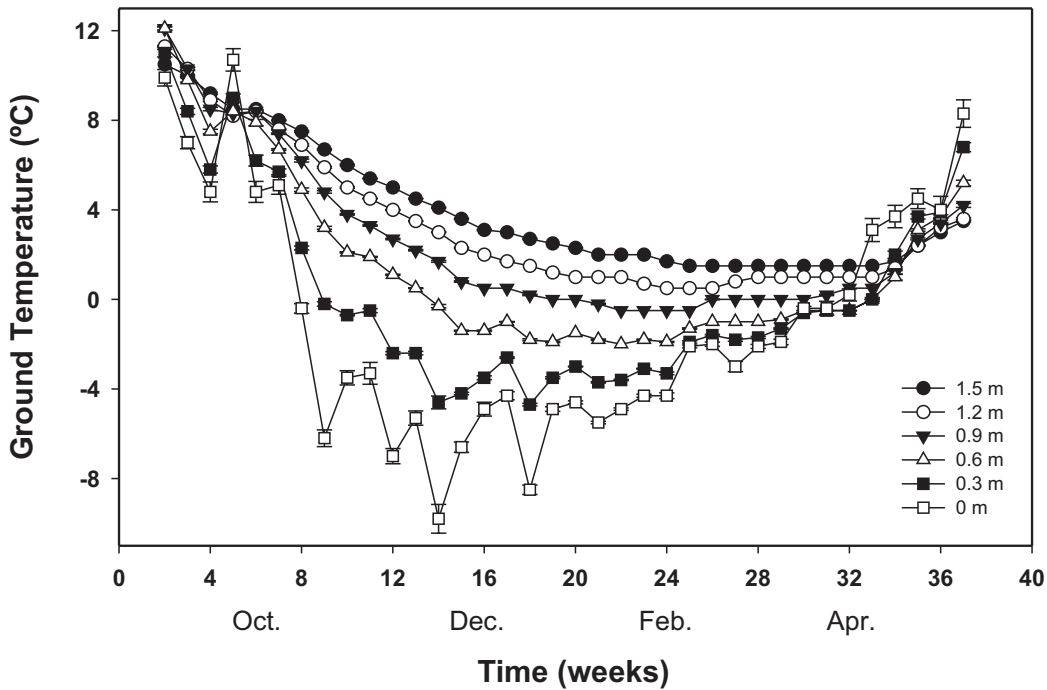
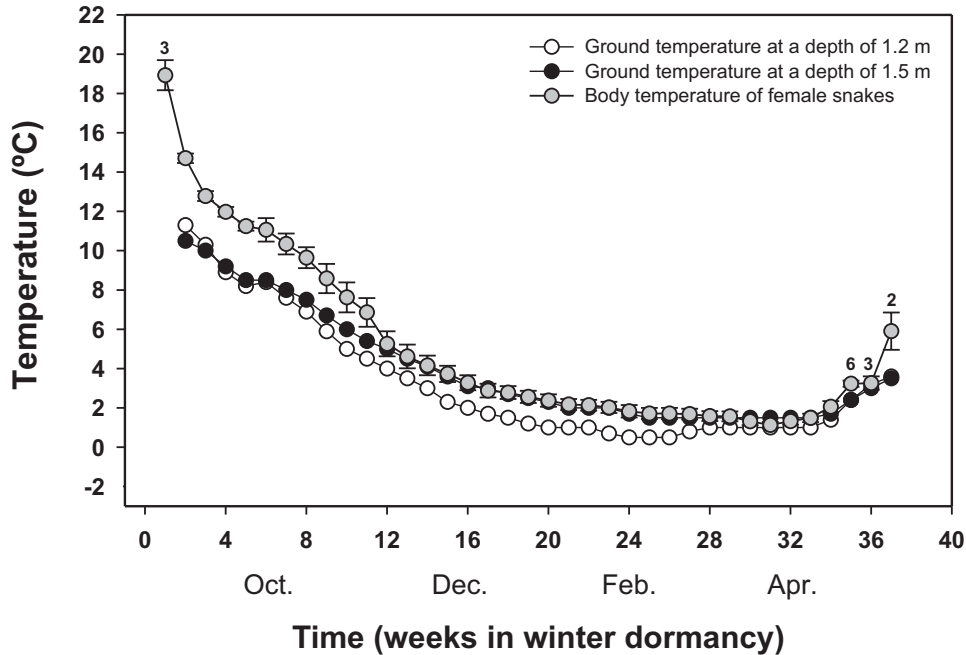


Fig. 4. Body temperatures of red-sided garter snakes during winter dormancy shown with ground temperatures at depths of 1.2 and 1.5 m. Unless otherwise noted by sample sizes above the SE bars, each data point for body temperature is a weekly mean \pm 1 SE of 7 snakes; ground temperatures are a weekly mean \pm 1 SE.



complete emergence must have been occupying shallower locations within the hibernaculum, and therefore were likely already in the process of emergence. (Although ground temperatures were recorded at a site approximately 20 km north of the den, we presume that ground temperatures do not differ greatly between these sites.) We currently have no way of estimating the time required for a snake to make its journey from the location of winter dormancy within the hiber-

naculum to the surface of the den. We hypothesize that the time required for complete emergence is highly variable among snakes and depends upon the position of each snake within the hibernaculum, as entrances into the den and the den itself are composed of narrow, rocky tunnels. Indeed, early versus late emergence from hibernacula has been correlated with snake depth in other studies (e.g., Carpenter 1953). Thus, increases in body temperature prior to emer-

gence (especially increases above ground temperatures at depths of 1.2 and 1.5 m) most likely reflect the vertical migration of snakes to the surface of the hibernaculum.

We speculate that critically low temperatures (i.e., 0.5–1 °C) may play a role in initiating snake emergence. For example, mean snake body temperatures were similar to those temperatures observed at a depth of 1.5 m from November through late April (from weeks 12–33; Fig. 4). However, the mean body temperature of snakes increased more rapidly than ground temperatures at this depth (Fig. 4), suggesting that snakes were vertically migrating to the surface of the hibernaculum during weeks 34–37 of winter dormancy. However, it again must be noted that ground temperatures were recorded at a site away from the hibernaculum. These observations suggest that when snakes reach a critical minimum temperature, they may be stimulated to change their vertical position in the den. Such critically low temperatures (and (or) the duration of exposure to low temperatures) may act as a Zeitgeber entraining an endogenous circannual cycle that governs spring emergence from winter dormancy.

There is precedence for vertical migration within hibernacula during winter dormancy in other ectothermic species. Sexton and Marion (1981) demonstrated that emergence of prairie rattlesnakes (*Crotalus viridis* (Rafinesque, 1818)) from winter hibernacula is regulated by a reversing thermal gradient within natural dens. In northern latitudes, where ambient temperatures can be below freezing during much of the winter, hibernating ectotherms select the warmest portion of the naturally occurring thermal gradient in the hibernaculum (Sexton and Marion 1981). Thus, in the early stages of winter dormancy, the cooling of the hibernaculum surface stimulates animals to migrate farther into the den. Vertical migration to the surface of the den occurs during the spring, when surface temperatures warm more quickly than the lower portions of the hibernaculum (e.g., Sexton and Marion 1981; Etheridge et al. 1983; Grobman 1990).

It is unlikely that the vertical migration of red-sided garter snakes within the den results from active behavioral thermoregulation, as snakes can emerge from winter dormancy at body temperatures of only 0.5 °C (Macartney et al. 1989; this study). Rather, vertical migration within and emergence from hibernacula may be regulated by a circannual cycle that is influenced by low temperatures. Because of the extreme environmental constraints on survival and reproduction in these northern populations of garter snakes, it is likely that a very sensitive mechanism regulating spring emergence has evolved in these populations.

Further research is necessary to determine the temperature threshold as well as the role of other environmental cues (e.g., humidity) in initiating vertical migration within and emergence from hibernacula. Studies of the spatial and temporal distribution of snakes in hibernacula, perhaps via artificial dens, would be particularly informative about the role of minimal overwintering temperatures in spring emergence. We are currently investigating how temperature cues interact with circadian and circannual hormone cycles to regulate spring emergence and reproductive behavior. Because male and female red-sided garter snakes demonstrate differential timing of emergence from winter dormancy, future studies examining possible sex differences in the mechanisms regulating spring emergence are needed. Such studies would pro-

vide much insight into the circannual rhythms and environmental cues regulating seasonality in ectothermic vertebrates.

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